Periodical Cicada: Sound Production and Hearing

Abstract. *The two main species intermingled in a brood of the 17-year cicada* (Magicicada) *have distinctive sound-making patterns and correspondingly different hearing abilities. Thus, they are acoustically isolated for mating purposes. Their simultaneous emergence and community "singing" has the important advantage of repelling predators.*

Since the discovery of the periodical cicada about three centuries ago, these insects have continued to attract attention by their sudden appearance in certain localities at intervals of 13 or 17 years, when for a few weeks they fill the air with their ear-piercing chorus of sounds, and then just as suddenly disappear. The sound-producing apparatus of the male was discovered early, and some time later the ears of both males and females were identified. Both these organs are the most remarkable of their kind among the insects.

It was established by Alexander and Moore in 1962 (*1*) that a typical brood of either the 13-year or 17-year type contains three distinct species, although one of the three appears to be poorly represented or possibly absent in some emergences. Many questions have arisen concerning the relations of these species in the groups, and especially the biological purposes served by their sound production.

In June 1970 the emergence in our area of a group of the 17-year type belonging to brood X made it possible to carry out studies of both the sound production and hearing in these insects. This population contained large numbers of *Magicicada septendecim* and *M. cassini*, but only a few *M. septendecula*, so that our observations are practically limited to the first two species.

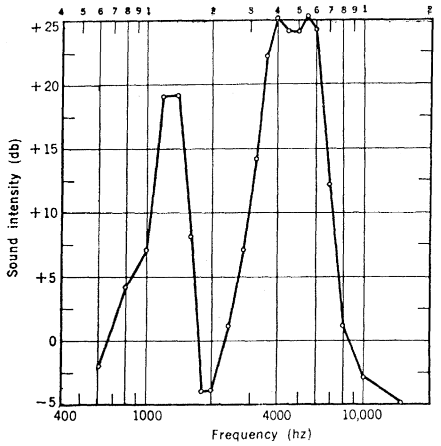

Fig. 1. The sound spectrum for a group of cicadas of brood X, *Magicicada.*

Tape recordings of the cicada sounds were made at a position on the ground beneath trees containing great numbers of the insects. The time was about midday with the sun shining, when the sound activity was at its peak. A spectrum analysis of the sounds was then obtained by playing the tapes to a wave analyzer with a pass band 200 hz wide with results shown in Fig. 1. Here is indicated the relative sound intensity in decibels over the range of frequencies from 600 to 15,000 hz. The distribution is strongly bimodal, with one peak at 1200 to 1500 hz and the other at 4000 to 6000 hz.

Recordings of the sounds produced by individual animals were then made in the laboratory. Individual *Magicicada septendecim* produced sounds with frequencies from 900 to 1600 hz, and individual *M. cassini* produced sounds with frequencies from 4500 to 6000 hz. The distribution of the frequencies produced by individuals of the two species thus accounts for the form of the sound spectrum obtained in the field.

It was found possible in the laboratory to elicit sound production by the males by presenting various noises and tones within a limited frequency range. The method varied for the two species. For *M. septendecim* a sound was presented and then stopped; the animal then produced its call, responding to the cessation of the sound. For *M. cassini* the animal responded to the onset of the sound, so that for these the stimulus was presented only briefly so as not to interfere with the recording of the insect's call. By stimulating with pure tones that were varied in both frequency and intensity it was possible to obtain a measurement of the animal's auditory range and sensitivity. Results for the two species are presented in Fig. 2. For *M. septendecim* the auditory responses occurred for a stimulating range from 600 to 3600 hz, with a sharp peak of sensitivity at 1500 hz. For *M. cassini* the range is from 600 to 10,000 hz with good sensitivity over the span of 2500 to 6000 hz; within this span there are two peaks at 3200 and 5800 hz.

The peaks of auditory sensitivity correspond closely to the peaks of sound production in these two species. For both sound production and hearing *M. septendecim* shows very narrow peaks in the region of 1500 hz, and *M. cassini* shows a somewhat broader form of curve, with a slight inversion in the middle of it, in a higher region of frequency.

It is clear that these two species of insects though thoroughly intermingled at the time of emergence from the ground and still considerably mixed in their movements through the trees, are well isolated in an acoustical sense. Each species best hears and responds to the sounds of its own kind.

Further studies involving a recording of the electrical output of the auditory organ have indicated that the selectivity present in the curves of Fig. 2 is achieved through a series of processes in which the nervous system plays an important part. In both males and females the peripheral response is rather broad, though with the best sensitivity between 1500 and 2500 hz for *M. septendecim* and between 2500 and 5000 hz for *M. cassini.* When nerve impulses are recorded from the ganglion to which the auditory nerve runs, the curve shows an increased degree of selectivity, and when (as in Fig. 2) the animal's motor activity is represented, which evidently involves still further neural processes, the selec-

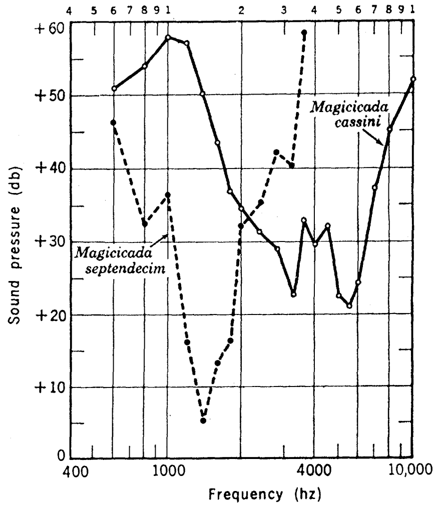

Fig. 2. Auditory sensitivity curves for two species of cicadas. The plotted points show for various pure tones the sound pressure, in decibels relative to 1 dyne/cm², required to arouse the activity of sound production by the insect.

tivity is much greater still. Hence it appears that the nervous system produces a considerable sharpening of auditory responsiveness—a neural action that has been assumed to occur in the discrimination of sounds in the auditory systems of man and other higher animals (*2*). This assumption has been made for the higher animals because in them—just as we find for the cicada—the peripheral actions of the ear show a much smaller degree of specificity than that exhibited in higher levels of performance. It is interesting to find the auditory nervous system performing this same role of the refinement of sensory information in animals so far apart in the biological series.

We now come to the question of the biological significance of sound production and hearing in the cicada. It was early appreciated that a function in mating is served. It was said at first that the female hears the sound produced by the male and seeks him out, but according to the extensive observations of Alexander and Moore the matter is more complicated. The males first react to one another and become segregated by species in particular sites in the tree tops. There they are joined by females of the same species, and mating takes place.

Still to be explained is the presence of two or more species in the emergence and thus in the general area before the sorting by species has been achieved. We offer the following hypothesis.

An emerging brood of cicadas encounters a serious problem of predation by birds. It has already been suggested that the coordinated emergence, within a few weeks, of millions of insects that have spent 13 or 17 years underground has the purpose of protecting some of the members from predation by the presence of overwhelming numbers. Sympatry of two or three species would of course contribute to the numbers. Still, a mere multiplication of one species would be just as effective.

Our observations on the behavior of predatory birds in two different localities containing large groups of cicadas have led us to another explanation. When a group is actively producing their sounds we find few birds in the area—often none in the center of the area and only a small number around the fringes. Certain birds—especially grackles—were observed to fly into the area, snatch a cicada, and at once fly away to eat it. When the sun was obscured by clouds, and sound production was less, there were more birds in the area and they stayed longer. In early morning or on cloudy days when the light was low and the temperature was depressed the sound production was feeble or absent. Then the birds entered the area freely and remained until they had gorged themselves.

Our theory is that the noise produced by the cicadas acts as a repellant to bird predators. It does so both because it is intense and thus painful to the ears and because it interferes with normal communicative processes among the birds. We measured the sound level on the ground beneath tall trees filled with singing cicadas as 800 dyne/cm^2. Obviously in the tops of the trees the level was higher, and must have reached 1000 dyne/cm^2 or more. For our ears this sound level is dangerously high. Some of us after spending several minutes in the area experienced ringing in the ears and partial deafness for some hours afterward.

If the cicada's sounds have a repellent effect on predators, the coexistence of two or three species becomes meaningful. Two species like *M. septendecim* and *M. cassini* with different frequencies of sound production can better jam the area acoustically than one species could by itself. The frequencies covered by the two peaks of Fig. 1 is just the range within which birds hear well; one of these peaks by itself would constitute much less annoyance and would leave some bird species relatively undisturbed.

Thus it seems to us that cicadas have developed a sympatric pattern of emergence involving two or three species whose sound productions are different and complementary so far as repellent effect is concerned, and that at the same time they have developed auditory capabilities that allow them to hear and respond to their own species exclusively. They are sympatric in sound production but isolated acoustically for mating purposes.

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References and Notes

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2. G. Von Békésy, *Experiments in Hearing* (McGraw-Hill, New York, 1960), pp. 535–547.
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Human Circadian Rhythms in Continuous Darkness: Entrainment by Social Cues

Abstract. *Three groups of two subjects each were kept in underground chambers, first for 4 days in an artificial light-dark cycle, and thereafter for 4 days in complete darkness. They lived on a rigorous time schedule. Physiological as well as psychological functions were measured at 3-hour intervals. There were no differences in the results between the two sections of the experiment. Social cues are sufficient to entrain human circadian rhythms, and absence of light has no immediate effect on the functions measured.*

There is ample evidence that diurnal rhythms are based on endogenous processes which have properties of self-sustained oscillations (*1*). Under constant conditions, the rhythm continues with a period which differs, in general, slightly from 24 hours—hence the term "circadian" rhythm (*2*). Under natural conditions, circadian rhythms are entrained to 24 hours by periodic factors in the environment, called entraining agents or *Zeitgebers*. Cycles of illumination intensity and, to a lesser degree, cycles of environmental temperature are the most important Zeitgebers for animals (*3*). It has been suggested that in man also light is an important Zeitgeber or that it is, at least, responsible for the entrainment of some human rhythms, such as that of the plasma level of 17-hydroxycorticosteroids (*4*). Prolonged darkness has been claimed to result in disappearance of the rhythm in some functions (*5*) or in immediate changes in the rate of increase or decrease: "The normal morning increase in urine and electrolyte excretion was much lessened by the absence of light, and its effects were apparent for the rest of the day"